NESTING AND PREDATORY BEHAVIOR OF SOME *TACHYSPHEX* FROM THE WESTERN UNITED STATES (HYMENOPTERA: SPHECIDAE)

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Abstract.— The first published observations on the nesting and predatory behavior of *Tachysphex antennatus* Fox, *T. occidentalis* Pulawski, *T. williamsi* Bohart, *T. yolo* Pulawski, *T. alpestris* Rohwer, *T. clarconis* Viereck, *T. apricus* Pulawski, and *T. cockerellae* Rohwer are presented herein. Also included are host and behavioral data on *T. tarsatus* (Say), *T. apicalis fusus* Fox, *T. similis* Rohwer, *T. ashmeadii* Fox, and *T. mundus exsectus* Fox.

The genus *Tachysphex* Kohl contains many rather small ground nesting species that utilize orthopterous prey. Nesting specifics are important in elucidating phylogenetic relationships in this large genus (Kurczewski and Elliott 1978). Some of the common eastern species have been studied extensively, but many western *Tachysphex* have never been observed. Biological data heretofore have been published for only 9 of the 46 western species (Krombein et al. 1979, Pulawski 1982). Thus, studies on western *Tachysphex* are needed to fill gaps in our understanding of the phylogeny and evolution of this large genus.

In this paper we bring together information accumulated on the behavior patterns of *Tachysphex* species from the western United States, along with prey records for several species based on museum specimens. Included are the first published notes on *T. antennatus* Fox, *T. occidentalis* Pulawski, *T. williamsi* Bohart, *T. yolo* Pulawski, *T. alpestris* Rohwer, *T. clarconis* Viereck, *T. apricus* Pulawski, and *T. cockerellae* Rohwer. In preparing the paper we have followed the nomenclature used by Krombein et al. (1979) and Pulawski (1982). The species are listed alphabetically by species group as in Krombein et al. (1979).

Pompiliformis Species Group

Tachysphex antennatus Fox

E. J. Kurczewski collected two females with prey at Erie, Pennsylvania, in 1981. Each made low, short flights. Both acridids were determined as nymphal *Melanoplus* sp.

Tachysphex apricus Pulawski

A paratype of this species, collected at Tucson, Arizona (W. Benedict), is pinned with a specimen of the phasmid *Parabacillus hesperus* Hebard, more than four times its length. We report this record, although Pulawski (pers. comm.) questions its authenticity.

Tachysphex occidentalis Pulawski

A paratype of this species, collected at 5500 ft at Antelope Spring, California, by M. E. Irwin, is pinned with a nymph of the acridid *Schistocerca shoshone* (Thomas).

Tachysphex tarsatus (Say)

Previus authors (Williams 1914, Evans 1970, Alcock and Gamboa 1975) reported females making single-celled nests and storing one, rarely two, large acridid nymphs (*Melanoplus* spp., *Trimerotropis* spp.). The first of two females collected at St. Anthony, Idaho, carried prey on the ground; the other carried prey in a series of short flights. We report the following prey records: *Dissosteira carolina* (L.) (Walworth, Wisconsin; 17 July 1913); *Melanoplus complanatipes* Scudder (1 mi SW Tom's Place, Mono Co., California; 13 August 1963; C. A. Toschi); 2 *Melanoplus* sp. nymphs (Erie, Pennsylvania; 13 July, 25

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August 1980; E. J. Kurczewski); *Pseudopomala brachyptera* (Scudder) nymph (Bath, Mason Co., Illinois; 3 July 1968; G. C. Gaumer); *Orphulella pelidna* (Burmeister), male (Closter, New Jersey; 16 July 1963; M. Statham). The last record is of the first adult prey reported for this species.

Tachysphex williamsi Bohart

A female collected at San Francisco, California, in May 1960 by J. A. Powell is pinned with a nymph of *Trimerotropis occidentalis* (Bruner) no larger than she. Another wasp from Cornish, Utah (27 July 1973; G. Eickwort and G. Bohart), identified as either this species or *T. tarsatus*, is pinned with a nymphal *Melanoplus sanguinipes* (Fabr.)

Tachysphex yolo Pulawski

One paratype was collected with a small nymph of *Melanoplus foedus* Scudder (St. Anthony, Idaho; 15 July 1977). The prey was being carried on the ground.

TERMINATUS SPECIES GROUP

Tachysphex alpestris Rohwer

A specimen from Morro Bay, California (J. A. Powell), is pinned with a nymphal acridid, *Oedaleonotus* sp.

Tachysphex apicalis fusus Fox

This species usually nests in sand cliffs (Kurczewski and Snyder 1968, Williams 1914), but Rau and Rau (1918) reported a female attempting to nest in the mortar of a building foundation and another starting a nest from an antlion burrow. One of us (F. E. K.) has observed this species searching in the openings between the siding shingles of a cottage. A female was observed at St. Anthony, Idaho (23 June 1979), digging in the soft sand of a previous excavation. When first seen, she was throwing sand out of the entrance. Upon completing it, she left the entrance open, oriented in a hovering flight, and flew away. Twice she returned without prey, hovered near the entrance, and flew off. When returning to the nest with prey, she landed nearby, although sometimes up to 1.5 m away, before resuming flight and carrying the prey directly into the open entrance. This wasp averaged 5.5 minutes between eight successive provisioning trips and 2 minutes within the nest between such trips.

The unfinished nest contained a single cell at the end of a burrow 7.5 cm long. This cell contained seven nymphal acridids; the female had been carrying an eighth when collected. Prey were placed head inward, venter upward or head inward, on the side. The prey were identified as *Melanoplus sanguinipes* (Fabr.).

Williams (1914) reported that one female of this species was unable to fly with a large grasshopper. He excavated a single-celled nest with two prey, but Kurczewski and Snyder (1968) reported that *T. a. apicalis* constructs multicelled nests, and stores several prey per cell.

Tachysphex clarconis Viereck

Four females were observed at St. Anthony, Idaho, during June 1979. One made 40 digging entries into the nest. The time spent inside increased as her digging progressed toward completion ($\bar{x}$ = 22.1 sec, first 10 entries; $\bar{x}$ = 31.3 sec, last 10), as did the time spent outside leveling sand ($\bar{x}$ = 12.2 sec, first 10; $\bar{x}$ = 29.0 sec, last 10). The female interrupted digging to chase away a satellite fly.

After removing and distributing the sand, this female walked around the entrance and threw sand back toward it. Periodically she took flight and hovered or perched on plants. After 3.5 min she reentered the nest and remained inside for 7.25 min. Then she temporarily closed the entrance, hovered 7.5 cm above the nest for a few seconds, flew in a circle, and landed before flying away. Total observation time was 44 minutes.

Prey were usually carried in flight directly to the nest area. A female would deposit her prey near the entrance, open and enter the nest, reappear headfirst, and pull in the grasshopper by its antennae. One female deposited her prey for about 10 minutes while searching for her nest. Then she located and opened the nest and took in the prey as described. The same female was later seen

carrying a rather large grasshopper in a series of short flights. During carriage the acridid's head protruded anteriorly beyond the wasp's. Three wasps stored from three to six grasshoppers per cell, as indicated by successive provisioning trips. Three acridids were recovered from one of the cells. Prey included *Melanoplus foedus* Scudder, nymph (1), and *M. sanguinipes* (8).

The only parasite observed, besides the miltogrammine fly, was a chrysidid, probably *Hedychridium* sp., seen digging into one of the nests while the wasp was away.

Tachysphex similis Rohwer

Two nests were excavated at Wamego, Kansas, in July 1968. One had a single cell with three prey; the other, four cells containing 3, 3, 5, and 3 prey. Prey used by *T. similis* at this locality included nymphs of *Melanoplus* sp. (8), *Mermiria* sp. (1), *Oplia obscurus* (Thomas) (2), and *Pseudopomala brachyptera* (Scudder) (8).

Undatus Species Group

Tachysphex ashmeadii Fox

This species was studied at Lakin, Kansas, in August 1964 and at St. Anthony, Idaho, in July 1977. We also include several new prey records from other collections. Our observations and previously published data indicate a greater range of variability in this species than is characteristic of many other *Tachysphex*.

Females started digging nests either from the sand surface or from preexisting depressions such as animal tracks. Digging wasps entered the burrow headfirst and threw sand backward with the forelegs while backing out of the nest to distances of 1.6 to 3.2 ($\bar{x}$ = 2.3) cm. One female made 21 entries from inception to completion of her nest; another, 25. The two wasps averaged 56 (4–159) seconds inside the burrow and 16 (6–40) seconds outside during digging and sand removal, respectively. There were no changes in duration of times as digging progressed. One female, digging in extremely hot sand, frequently left the nest and flew to nearby vegetation. She flew backward out of the nest, throwing the sand behind her, and averaged only about half as long on the sand surface as had other females.

Wasps left their entrances open while hunting. They also left intact the ovoidal-elongate tumuli that accumulated during digging. One such tumulus was 5 cm long, 3 cm wide, and 0.5 cm high. Following completion of the burrow, females walked around their entrances and sometimes reentered. They then made low flights above the site and flew to nearby vegetation to hunt. Females made the most rapid hunting movements of all *Tachysphex* we have observed. Periodically they returned without prey and reentered their burrows. One such female returned four times: 5, 29, 33, and 105 minutes after she first left to hunt. Some females dug within the entrances during these returns.

Previous records (Williams 1914, Evans, pers. comm.) and many of our own observations indicate that females of *T. ashmeadii* usually prey on large acridids in the late nymphal or adult stage and transport them to the nest on the ground. However, we have seen females carrying smaller prey (up to 2.2 times the wasp's weight) directly into the nest in flight, while holding the prey's antennal bases with the mandibles. Times between provisions ranged from 22 to 178 ($\bar{x}$ = 106; n = 5) minutes. Females using more than one prey per cell spent an average of 2.5 minutes inside their nests before leaving to hunt again.

Nest dimensions for three burrows at Lakin, Kansas, were as follows: burrow length: $\bar{x}$ = 9.6 (8.9–10.4) cm; cell depth: $\bar{x}$ = 5.3 (5.0–5.9) cm. These nests were single celled, and each contained a single grasshopper (weights: 59, 200, and 232 mg). Williams (1914) and Alcock and Gamboa (1975) also reported a single prey per cell, but two single-celled nests in Idaho each contained two prey. In one the egg was on the larger grasshopper, which was taken into the nest last. H. E. Evans (pers. comm.) excavated a nest of this species at Rodeo, New Mexico, and found a single prey bearing an egg in the distal burrow rather than in the cell.

TABLE 1. Prey of *Tachysphex ashmeadii*.

Species	State of collection	Source or collector
Agenceotettix deorum (Scudder)	KS, WY	Williams 1914, Lavigne and Pfadt 1966
Arphia sp.	ID	NBE
Bruneria sordida (McNeill), nymph	ID	NBE
Cordillacris crenulata (Bruner), adult	KS	Williams 1914, Krombein et al. 1979
Cordillacris occipitalis (Thomas)	WY	Lavigne and Pfadt 1966
Melanoplus bivittatus (Say) ?	KS	FEK
Melanoplus lakinus Scudder, nymph	AZ	P. Rauch
Melanoplus sanguinipes (Fab.)	ID	NBE
Melanoplus sp., nymph	CO, AZ	G. C. Gaumer, G. and K. Eickwort
Metator sp., nymph	—	Krombein and Burks 1967
Opeia sp., nymph	—	Krombein and Burks 1967
Orphulella sp., adult	TX	R. E. Acciavatti
Phlibostroma sp., adult	—	Krombein and Burks 1967
Trachyrhachys kiowa (Thomas), male	KS, WY	Williams 1914, Lavigne and Pfadt 1966
Trimerotropis sp., nymph	KS	FEK
Trimerotropis bilobata Rehn & Hebard, male and nymph	ID	NBE
Trimerotropis pallidipennis (Burm.), adult and nymph	TX	J. E. Gillaspy

Prey collected in Kansas were invariably placed venter upward, head inward, but Alcock and Gamboa (1975) reported lateral placement from a nest in Arizona. Eggs were laid on either side, transversely between the prey's pro- and mesothoracic legs.

Acridids from 11 genera have been preyed upon by this species (Table 1).

Brullii Species Group

Tachysphex mundus exsectus Fox

One female was collected with a nymph of a tettigoniid, *Conocephalus* sp., at Wamego, Kansas, in July 1968 (G. C. Gaumer). Kurczewski (1979) has described the nesting behavior of this species, which also occasionally preys on gryllids.

Julliani Species Group

Tachysphex cockerellae Rohwer

A specimen from Napa Co., California (D. & W. Dunenmacher), is pinned with a nymph of the mantid, *Litaneutria minor* (Scudder).

Discussion

Krombein et al. (1979) divided the North American species of *Tachysphex* into five species groups, based on morphological criteria. Our studies, especially those on members of the Terminatus species group, show that behavioral traits may also characterize these groups.

Members of the Terminatus group usually nest in flat sand, except for *T. a. apicalis* and *T. apicalis fusus*, which nest in sand cliffs (Kurczewski and Snyder 1968). All species construct multicelled nests which are provisioned with small, nymphal acridids. Since the prey are small, they are usually carried to the nest in flight, and several are used to stock each cell. Species in this group close the nest while hunting, after elaborately leveling the tumulus, except for the subspecies of *T. apicalis*, whose vertical nesting sites preclude this behavior (Kurczewski and Snyder 1968). Nesting behavior of *T. clarconis*, reported here for the first time, supports its placement in the Terminatus group because it shares this set of nesting components.

All previously studied members of the Brullii group prey upon orthopterans other than acridids. *Tachysphex alayoi* Pulawski preys upon blattids (Pulawski 1974, Elliott et al. 1979), and *T. belfragei* and *T. mundus* prey mostly upon tettigoniids (Krombein et al. 1979, Kurczewski 1979). *Tachysphex coquilletti* Rohwer, the only previously studied North American species of the Julliani group, preys upon mantids (Alcock and Gamboa 1975). Our report of mantids as prey of

T. cockerellae substantiates its placement in this group.

The large Pompiliformis group now contains 44 North American species (Krombein et al. 1979, Pulawski 1982). Many species in this group also share a suite of similar behavioral traits, including the making of single-celled nests, utilizing one or a few large prey per cell, carrying prey on the ground, leaving the nest open while hunting, and not leveling the tumulus (Kurczewski 1964, Williams 1914). Although Krombein et al. (1979) placed *T. ashmeadii* in the Undatus group, components of its nesting behavior match very closely those described above. This suggests that *T. ashmeadii* has close affinities with the species in the Pompiliformis group.

Studies on certain species in the Pompiliformis group, however, indicate considerable variation in behavior. *Tachysphex pechumani* Krombein demonstrates many of the group's characteristics but makes a rudimentary temporary closure. Based on its morphology and behavior (Kurczewski et al. 1970, Kurczewski and Elliott 1978), we have suggested that this species occupies a unique phylogenetic position intermediate between the Terminatus and Pompiliformis species groups. *Tachysphex krombeini* Kurczewski makes single-celled nests but stores several small acridids and tettigoniids, mixed, and carries them to the nest in flight (Kurczewski 1971). *Tachysphex krombeini* is the only Nearctic species in the group that preys on families other than Acrididae. Should the record of *T. apricus* preying on phasmids be substantiated, this would further increase the range of prey families reported for this group. We also report that females of *T. yolo* and *T. williamsi* use rather small prey in comparison with many previously studied members of the group. It is probable that further studies of species in this group will identify affinities in behavior that separate the large group into several smaller ones. Pulawski (1982) noted that, morphologically, the group is less distinct than other species groups of *Tachysphex* and has suggested the grouping may be artificial.

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W. J. Pulawski, California Academy of Sciences, determined the *Tachysphex* species. Prey were determined by A. B. Gurney, USDA, Systematic Entomology Laboratory; M. A. Brusven, University of Idaho; D. C. Rentz, CSIRO, Canberra, Australia; and I. J. Cantrall, Museum of Zoology, University of Michigan.

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